Temporal variation of litter decomposition in relation to simulated soil climate. Long-term decomposition in a Scots pine forest. V

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Received July 6, 1984

JANSSON, P.-E., and B. BERG. 1985. Temporal variation of litter decomposition in relation to simulated soil climate. Long-term decomposition in a Scots pine forest. V. Can. J. Bot. **63**: 1008–1016.

Decomposition of Scots pine needle litter was studied in a Scots pine forest in central Sweden. A 6-year series with annual incubations of needle litter was used to analyse the climatic influence on the process. The original litter was of similar chemical properties between years and each year new litter was incubated, in the same way, in the autumn. Sampling took place at time intervals ranging from 1 month to 1 year. Soil climate variables such as temperature and water contents and tensions were calculated with a soil water and heat model from standard meteorological data. Decomposition rates from periods longer than 145 days were correlated with different soil climatic factors. The responses for the 1st and 2nd incubation years were not significantly different, but higher coefficients of determination (r^2) were found for the 2nd year. Estimated actual evapotranspiration or soil temperature explained temporal variation of decomposition to about 70%; soil water content only or soil water tension only explained 90%. When moisture and temperature were combined, 95 and 99% of the variation could be explained for the 1st and 2nd year, respectively. When time periods down to 1 month were included, very poor fits were found with the same climate response functions. However, the relationships were improved by an inertia function which indicated a time lag of 2–3 months between soil climate and the response in decomposition rate.

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La décomposition de la litière d'aiguilles de pins sylvestres a été étudiée dans une forêt située au centre de la Suède. Une série de données de 6 ans, comprenant des incubations annuelles de litières d'aiguilles, a servi à analyser l'influence du climat sur le processus de décomposition. La litière nouvelle présentait les mêmes propriétés chimiques d'une année à l'autre et, chaque année, de la litière nouvelle a été incubée à l'automne selon un protocole identique. Des échantillons ont été prélevés à des intervalles s'étendant de 1 mois à 1 an. Les variables climatiques du sol, telles que la température, la teneur en eau et la tension hydrique, ont été calculées à partir de données météorologiques courantes, à l'aide d'un modèle sur l'eau et la chaleur dans le sol. Les taux de décomposition pour les périodes plus longues que 145 jours ont été mis en corrélation avec diverses variables climatiques du sol. Les réponses pour la 1^e et la 2^e années d'incubation ne sont pas statistiquement différentes, mais les coefficients de détermination (r^2) sont plus élevés pour la 2^e année. L'évapotranspiration estimée ou la température du sol expliquent jusqu'à environ 70% de la variation temporelle de la décomposition, alors que la teneur en eau ou la tension hydrique du sol expliquent chacune, individuellement, 90% de la variation. L'humidité et la température combinées expliquent 95 et 99% de la variation pour la 1^e et la 2^e années, respectivement. Lorsque des périodes plus courtes, jusqu'à 1 mois seulement, sont incluses, les mêmes fonctions de réponse au climat donnent des ajustements très pauvres aux données. Cependant, les relations sont améliorées par une fonction d'inertie prévoyant une période de latence de 2 à 3 mois entre la mesure des conditions climatiques du sol et la réponse du taux de décomposition.

[Traduit par le journal]

Introduction

Good knowledge is needed of how factors such as temperature and moisture influence the decomposition process if measurements of decomposition are to be used in analysing biological or chemical changes in natural ecosystems. The litter-decomposing microorganisms are dependent on temperature and moisture for their activity, which determines the decomposition rate of litter. Other important factors are nutrient levels and availability of the carbon source. Several studies, especially in the laboratory, have been made to correlate the microbial activity measured as CO_2 release or O_2 consumption, to temperature and moisture in, e.g., soil cores, and Bunell *et al.* (1977) presented such a study where they measured respiration from tundra leaf litters of different ages. They consequently included the changing substrate quality and could thereby explain between 70 and 90% of the variability of respiration. In their model the Q_{10} factor varied with the substrate and ranged from 8.8 for newly formed litter to 1.8 for old litter.

Several models for respiration which are dependent on moisture and temperature have been constructed from laboratory measurements, but apparently few have been made from field data (cf. Svensson 1980). There are, of course, several problems involving the construction of a soil respiration model from field data. Apart from good field registration of temperature and moisture conditions there are also problems connected with, for example, root respiration and determination of actual volumes of respiration flasks.

It appears that few attempts have been made to correlate field data of litter decomposition to soil temperature and moisture conditions. Regional climatic variables, such as calculated actual evapotranspiration, have been used with success to explain large-scale variability (Meentemeyer 1978), but the high between-year variation found at one site for litter decomposition in central Sweden could only partially be explained by such variables (B. Berg and V. Meentemeyer, unpublished).

This paper presents a method to analyse the variability found in a 6-year series of needle litter decomposition with consecutive annual incubations. For this we used estimated values

of actual daily means of soil temperature and soil moisture content or tension. The daily soil climatic conditions were calculated with the aid of a coupled soil water and heat model (Jansson 1980) requiring standard meteorological driving variables. The variation in litter mass loss between summer and winter periods and between years for litter up to 2 years of age is compared with the variation both of soil climate and of actual evapotranspiration. Different expressions have been used to test the relative importance of the different abiotic variables and to find which expressions give the best agreement with observed litter decomposition. For the present study, litter was incubated in so-called litterbags. It has been argued that mass loss studies from litterbags should be used only for comparisons, but even if the mass loss values obtained should not be regarded as absolute, they may still be used in, e.g., simulation models, where more principles than absolute values are required (Wieder and Lang 1982). In the present paper we do not intend to suggest that absolute values were obtained and the aim is to present a model with relative mass loss versus temperature and moisture. In preceding papers we dealt with the same material with regard to organic chemical changes (Berg *et al.* 1982) and nutrient dynamics (Staaf and Berg 1982).

Site description

The 120- to 130-year-old Scots pine stand studied is located at the Swedish Coniferous Forest Project research site, Ivantjärnsheden, central Sweden (60°49′ N, 16°30′ E), at an altitude of 185 m on a flat area of deep glacifluvial sand sediments. The mean annual precipitation at a nearby village is 609 mm (1931–1960) and the mean annual temperature is +3.8°C. The length of the growing season is about 160 days (number of days with a daily temperature higher than 6°C) (Axelsson and Bråkenhielm 1980).

The tree layer is exclusively composed of *Pinus silvestris* L. and has a density of 393 trees per hectare and a height of 17–19 m. *Calluna vulgaris* and *Vaccinium vitis-idaea* form a well-developed field layer, and the bottom layer, completely covering the ground, is mainly composed of the mosses *Pleurozium schreberi* and *Dicranum rugosum* together with *Cladonia* lichens. The most recent direct effect of forestry practices was a slight thinning in 1960. A more complete description is given by Axelsson and Bråkenhielm (1980).

The soil profile is an orthic humoferric podzol (iron podzol) with a weakly developed A_e horizon (bleached horizon; 2–7 cm) and the humus form is a typical mor. A very loose L horizon (A_{00}), interwoven with living mosses and lichens, covers an F–H horizon ($A_{01}-A_{02}$) of 5–10 cm. The F horizon (A_{01}) and the H horizon (A_{02}) are almost indistinguishable from each other. The pH range is 3.9–4.2 in the F–H horizon and 4.6–4.8 in the upper mineral soil. The parent mineral material as well as the whole soil are considered to be very poor in essential nutrients. The C/N ratio of the F–H horizon ($A_{01}-A_{02}$) is 42.

Materials and methods

Needle collection, storing, weighing, field incubations, and site description

Needle litter was sampled at Invantjärnsheden in the autumns of 1973 to 1979 from the branches of trees in a stand that was about 15 years old. Brown needles from the falling needle generation were taken at abscission from trees growing in an area of about 20 × 50 m and were stored at −20°C until sample preparation took place.

Before weighing, the needles were air dried at room temperature to about 5–8% moisture. Dry mass was determined at 85°C and the largest difference in moisture content was less than ±0.5% of the average (n = 20).

The litter bags, made of Terylene net with a mesh size of about 1 mm, measured 8 × 8 cm. About 0.6–1.0 g of needle litter was enclosed in each bag. The litterbags were placed on the litter (L) layer in a measurement plot (1 × 1 m) in each of 20 blocks in a randomized block design in the stand (3 ha). They were fastened to the ground by 10 to 15 cm long metal pegs.

The incubations started in May 1974 and in October of the years 1974 to 1979 and samplings were made three or four times annually (Appendix 1). On each sampling occasion one sample from each of the 20 blocks was collected. Only mean values from these 20 blocks are considered in the following. The litterbags were transported directly to the laboratory and cleaned of moss, lichen, and dwarf shrub remnants. After drying at 85°C they were weighed individually.

The abiotic SOIL model

The SOIL model consists of the two coupled partial differential equations for heat and water which enable predictions of the soil climate at any level in the soil profile with appropriate soil properties and boundary conditions specified. A detailed description of the model with all equations, parameters, and numerical methods is given by Jansson and Halldin (1980). A brief summary of the model is given here in Appendix 2. The model has previously been adapted to the 120-year-old Scots pine forest in Jädraås and tested against measurements of temperature, snow and frost depths, and soil water content and tension (Jansson and Halldin 1979).

For the present study the model was run for 6 full years and daily means of soil temperature and water content and tension were predicted representing the organic soil layer as a whole (Fig. 1).

Coupling of simulated soil variables and litter decomposition

The temperature effect on litter decomposition rate was tested with the commonly used Q_{10} equation:

$$[1]\quad D_T = Q_{10}^{((T - T_n)/10)}$$

where D_T is a multiplicative factor for decomposition, Q_{10} is the steepness in the temperature function, T is actual soil temperature, and T_n is the temperature for which D_T equals 1.

The soil moisture effect was treated separately with expressions either of the unfrozen water content, (D_θ), or of the soil water tension, (D_Ψ):

$$[2]\quad D_\theta = \begin{cases} (\theta/\theta_o)^a & \theta \le \theta_o \\ 1 & \theta > \theta_o \end{cases}$$

$$[3]\quad D_\Psi = \begin{cases} (\Psi_o/\Psi)^b & \Psi > \Psi_o \\ 1 & \Psi \le \Psi_o \end{cases}$$

where θ is the volumetric water content, θ_o is the threshold water content to achieve the optimal decomposition rate, Ψ is the soil water tension expressed in centimetres water, Ψ_o is the threshold water tension to achieve the optimal decomposition rate, and a and b are empirical constants.

These simple mathematical expressions were selected because only drought and not excess of moisture was believed to reduce decomposition in the extremely well drained sandy soil at Jädraås.

Actual decomposition (litter mass loss) was expressed as the daily mean rate in percent of the total mass of litter in the beginning of each subperiod from which measurements existed. These values of decomposition rates were compared with different abiotic functions such as the products of D_T and D_θ or D_T and D_ψ or the mean actual evapotranspiration. The relationships between the decomposition rates and abiotic functions were fitted to linear equations and the coefficients of determination were used as a measure of goodness of fit. The sensitivities for a number of different values of Q_{10}, θ_o, a, ψ_o, and b were tested on these coefficients of determination. The data set was used with either the 1st-year decomposition values only, those of the 2nd year only, or of both years together.

In a first step, only decomposition data for periods of at least 4 months were used. In a second step all observations of decomposition were used independent of the length of the period for observation. To obtain a better fit between the abiotic functions and the observed decomposition an inertia was introduced in the daily values of abiotic functions with the equation

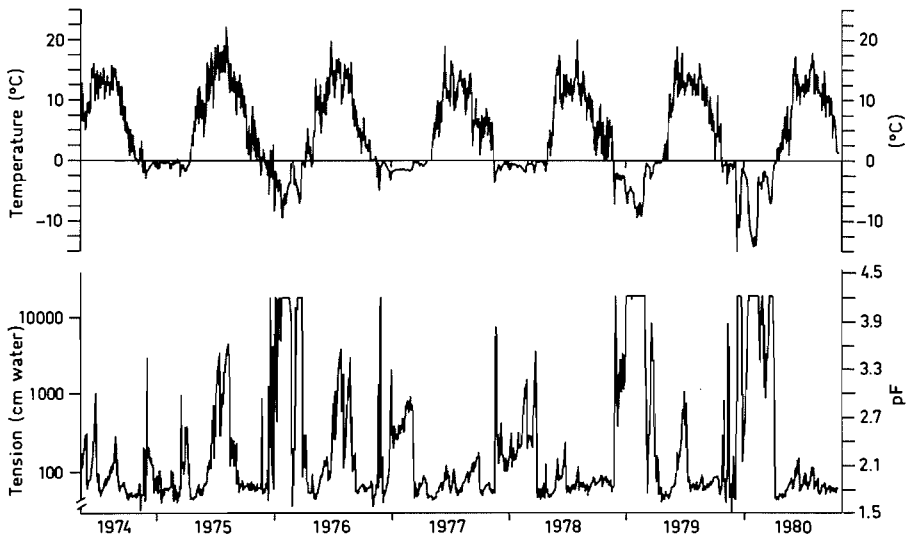

FIG. 1. Simulated soil temperature and water tension during 7 years in the organic soil layer (L + F−H) in a 120-year-old Scots pine forest.

[4] $A(t) = d \cdot (D(t) - A(t - 1)) + A(t - 1)$

where A denotes the adjusted abiotic function at the present day (t) or the preceding day ($t - 1$), d is the damping coefficient, and D denotes the unadjusted abiotic function.

Results and discussion

General comments on the incubation of needle litter in the system

Decomposition studies with incubation of litter in litterbags have been suggested to give either somewhat lower mass loss rates as compared with other incubation methods tested (Witkamp and Olson 1963) or higher rates (Towpasz 1976). Such effects could probably be ascribed to the type of litterbag material used, an observation made and discussed by Lousier and Parkinson (1976). In a system with litter-consuming soil animals present one could expect that a lower rate would be the result if these were without access to the litterbag litter.

In our system the litterbags were big enough to allow free passage for the few types of existing animals and they could thus exert their influence on the decomposition rate. It appears, however, that their influence was so low that we may regard the present investigation as an evaluation of the microbial activity only (Berg *et al.* 1980).

The litter bags became grown through and over with moss and cowberry shrub in the first half year and were thus observed at a more shallow level in the profile than were single needles after the same time (Berg 1977). To estimate the difference in mass loss rate between the position on the L layer (on the moss) and just below it (on the F−H layer) a separate measurement was carried out (Table 1). The differences in mass loss between the positions were small and the maximum difference observed was 3−4% units after 2 years incubation with the lower rate in the lower position.

We may conclude that if we relate decomposition rate in the moss layer to soil climate of the F−H layer, the deviations should not be unacceptable.

The incubations

Most of the needle litter sets (B−F) were incubated in the autumn at litter fall and we have preferred to use mass loss values from these sets, whereas the only mass loss value used for set A was that for the first summer. The reason was that we wanted a uniformity in incubation times versus climate and time for fungal ingrowth, which is slow (Berg and Söderström 1979). It was also more realistic with respect to the forest where 90% of the needle litter falls in the autumn. The chemical composition which changes strongly with the ongoing decomposition (Berg *et al.* 1982; Staaf and Berg 1982) affects the litter decomposition rate (Berg and Ågren 1984), but we have not included this in the present analysis. To avoid problems with differences in litter quality we used data from the first 2 years only and before the changes had become too large.

TABLE 1. Comparison of mass loss of needle litter under decomposition in the L and F−H layers of a 120-year-old Scots pine (*P. silvestris*) stand at Ivantjärnsheden. Measurements began May 12, 1974. Standard errors are given in parentheses

		Mass loss (% of initial mass)	
Date	Days	L layer	F−H layer
May 12, 1974	0	0(0)	0(0)
October 29, 1975	545	43.2(1.1)	39.2(1.1)
April 4, 1976	726	44.5(0.8)	44.3(1.5)
August 25, 1976	845	51.2(1.2)	48.1(1.6)

The soil climate

The 6 complete years of predicted soil climate (Fig. 1) represented a substantial variation with respect to soil moisture and temperature. Two summers, namely 1975 and 1976, can be characterized as rather warm with extended drought periods, whereas all other summers were moist except for a drought period in May and June in 1979. The variations of soil temperatures were much more pronounced between different winters than between summers. Three winters, namely 1975−1976, 1978−1979, and 1979−1980, had soil temperatures well below 0°C which also caused high water tension in the soil. The other winters were both moister and warmer, mainly because of thicker snow packs which prevented the soil becoming completely frozen. Under these conditions some water was always unfrozen.

Decomposition rate as a function of soil climate

In the first attempt we used only mass loss data which were significantly different, which in practice implied that only mass

TABLE 2. Comparison of coefficients of determination (r^2) obtained when correlating observed decomposition rates to different estimates of climatic influences as independent variables

Independent variable	First incubation year (n = 9)	Second incubation year (n = 8)	Both years (n = 17)
Actual evapotranspiration (AET)	0.41	0.74	0.55
Soil temperature	0.37	0.77	0.52
Soil water tension	0.78	0.97	0.81
Soil water content	0.68	0.96	0.77
Soil temperature and water tension	0.90	0.98	0.89
Soil temperature and water content	0.85	0.99	0.87

losses for periods longer than 145 days were used. These were related to climate by linear regression. In Eq. 1 to Eq. 3, different values of the parameters Q_{10}, θ_o, a, ψ_o, and b were used to obtain the best coefficient of determination for the linear regressions where the soil climate was treated as an independent variable. The moisture factor, expressed either as a function of the volumetric content or as tension, could explain more of a temporal variation than could temperature only or actual evapotranspiration (Table 2).

The two different relations obtained for the 1st and for the 2nd incubation year, respectively, were never significantly different either with respect to slope or level. Nevertheless, it was quite obvious that for all different abiotic measures they were better related to the 2nd year of decomposition than to the 1st year (Table 2). There are at least two reasons that could explain the better fits for the 2nd year of decomposition. First a small fraction of the litter can be leached from the substrate because of water-soluble substances (Nykvist 1963). This fraction is also influenced by freezing and thawing and can therefore be important for fresh litter during the first winter. In a laboratory study Bogatyrev *et al.* (1983) found, for the litter type used in this study, a total mass loss of 1.3% after 13 consecutive cycles of leaching, including one freeze–thaw cycle. This fraction was about 10% of the total amount of water-soluble substance.

The second reason is a delayed ingrowth of fungal biomass which influences the decomposition rate in the opposite direction during the 1st year. Berg and Söderström (1979) measured live plus dead mycelium and found that the heavy increase took place in the 1st year. This was also seen (Wessén and Berg 1983) for live (FDA) mycelium. Visser and Parkinson (1973) found that depending on moisture conditions no really effective ingrowth of fungal mycelium took place in decomposing aspen leaves until after 2–3 weeks in the field, and still after about 2 months the increase continued. In our case, it thus appears reasonable to assume (*i*) that we may have a slow ingrowth and (*ii*) that the amount of ingrown mycelium may depend strongly on the climate in the first autumn. With different amounts of mycelium in the litter we may expect very different magnitudes in response to climate. It is thus not only the higher level of mycelium that determines the response but also the possibility that the ingrowth may be delayed initially in the 1st year. We may speculate on a further factor which may delay the response in decomposition to changes in temperature or moisture, namely the succession of fungal species. The chemical composition changes in the 1st year are very strong as compared with those in the later years (cf. Berg *et al.* 1982). We may thus expect that the fungal species dominating in the early stages, consuming more readily available carbon sources, at least partly should be replaced by, for example, basidiomycetes (Swift *et al.* 1979). Even if fungal species of different successional steps may be found in the decomposing material simultaneously, it should take some time for a shift between successional steps to take place. Since it appears that the chemical changes are more drastic in the 1st year, we may expect more such influences in this time period. The change in substrate quality which has taken place between the years (Berg and Ågren 1984; Berg and Staaf 1980) was of course not similar for all samples and may be behind the unexplained part (2–15%) of the decomposition in the two 1st years (<50% mass loss). It appears, though, that for this litter the more retarding changes take place later (Berg and Ågren 1984).

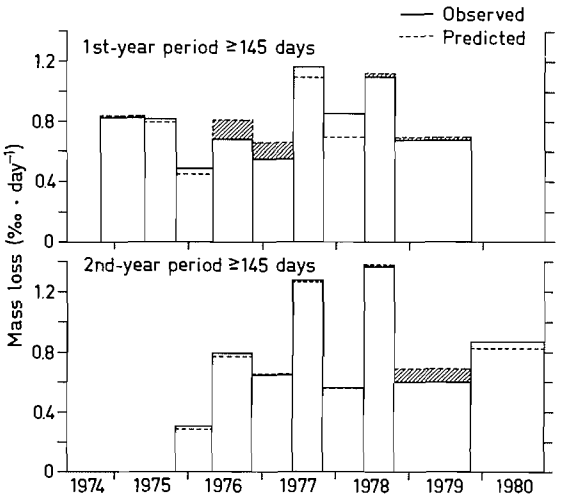

FIG. 2. Observed decomposition rates for periods longer than 145 days for both the 1st and 2nd year of decomposition compared with predicted litter mass loss. The empirical coefficients estimated from the same data. Shaded area shows underestimated mass loss.

When the best linear relationships for the 1st and the 2nd incubation year were used separately, good agreements were obtained between predicted and observed decomposition (Fig. 2). The agreement was better for the 2nd incubation year than for the 1st. This seems to be an effect of leaching from fresh litter during the winter and a delayed ingrowth of fungal biomass in the summer (see discussion above). Observed rates from the 1st year were compared with observed rates from the 2nd year, higher in decomposition rates during the winter and lower in rates during the summer. The sensitivity of the coefficient of determination for different choices of values on Q_{10}, θ_o, and a showed that the best regression was obtained with a low Q_{10} value, namely 1.3, for θ_o a value of 28 vol. %, and an a-value of 3 (Fig. 3). When data from the 1st incubation year were used, a similar sensitivity was obtained when Eq. 3 with water tension instead of Eq. 2 with water content was used in combination with Eq. 1 (Fig. 4). In both cases the best fits were obtained with Q_{10} values around 1.3 to 1.6. It was, however, noted that high values for the coefficient of determination were mainly found when the linear form of Eq. 3 was used but not with a linear form of Eq. 2.

Also for the 2nd year of incubation the sensitivity of the coefficient of determination for changes of values of the same parameter values was similar to that of the 1st year of incubation. The Q_{10} values giving the best fits were still very low,

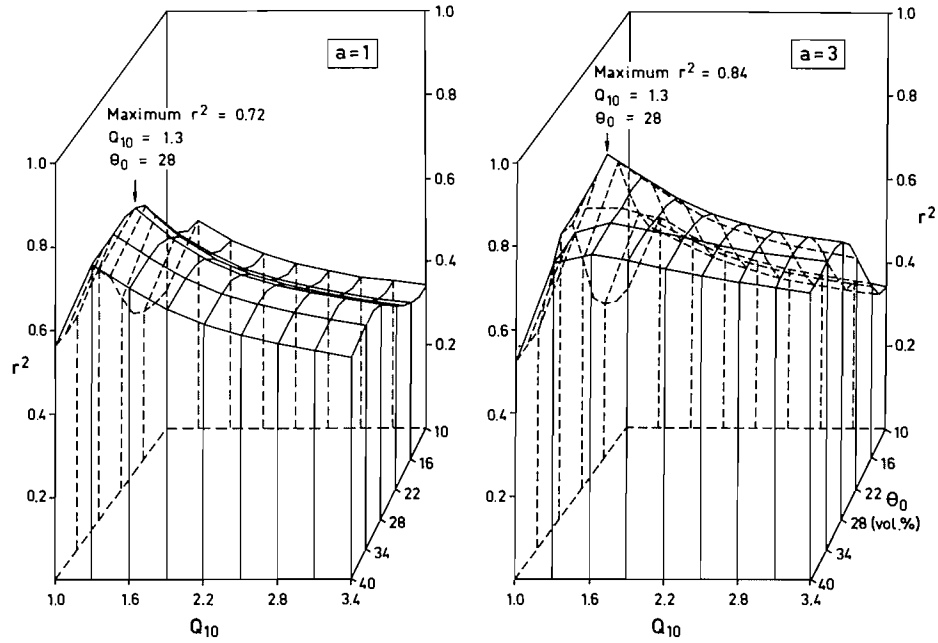

FIG. 3. Coefficients of determination (r^2) obtained with linear regression between observed decomposition rates (1st year only) and the product of Eq. 1 and Eq. 2 reflecting water content, for different values of Q_{10}, θ_o, and a. Only time periods exceeding 145 days were accepted.

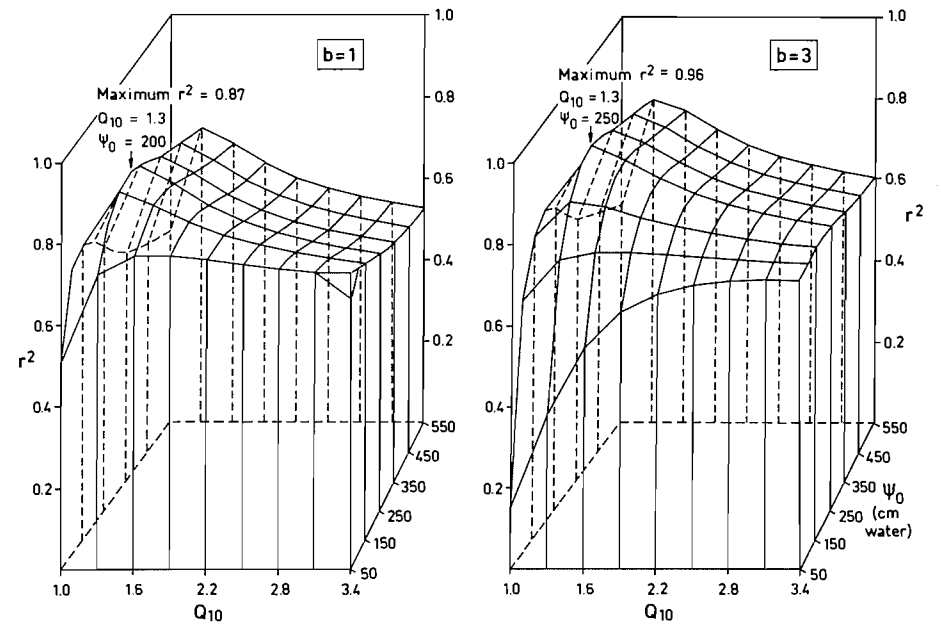

FIG. 4. Coefficients of determination (r^2) obtained with linear regression between observed decomposition rates (1st year only) and the product of Eq. 1 and Eq. 3 reflecting water tension for different values of Q_{10}, ψ_o, and b. The same data were used as for the graph of Fig. 3.

around 1.3 to 1.6, but it was obvious that high values for the coefficient of determination could be obtained for a wide range of both Q_{10} and the other parameters in the moisture equations. When data for short periods were excluded, the total material only comprised 9 and 8 mass loss values for the 1st and the 2nd years, respectively, and care must be taken when interpreting the sensitivity of parameters in the climatic equations. The parameters which gave the best linear relationship for these data may not be the same as those actually controlling the decomposition rate in a short-term perspective.

When all the decomposition periods were used, independently of period length, a very poor agreement was obtained between predicted and observed mass loss (Fig. 5). This was emphasized for the 1st year of decomposition where the number of periods observed increased from 9 to 15. The coefficient of determination decreased from 0.84 to 0.10, which means that the latter was not significantly different from zero. This was found when the same parameter values as those obtained from longer periods were used, but a new trial to find better relationships by changing parameter values in Eq. 1 to Eq. 3 was unsuccessful. However, a typical pattern with overestimation of the decomposition in the beginning of the growing season and an underestimation in the late autumn was observed, which suggested a lag in the climatic effect on decomposition.

The change of fit for the 2nd year of decomposition is not

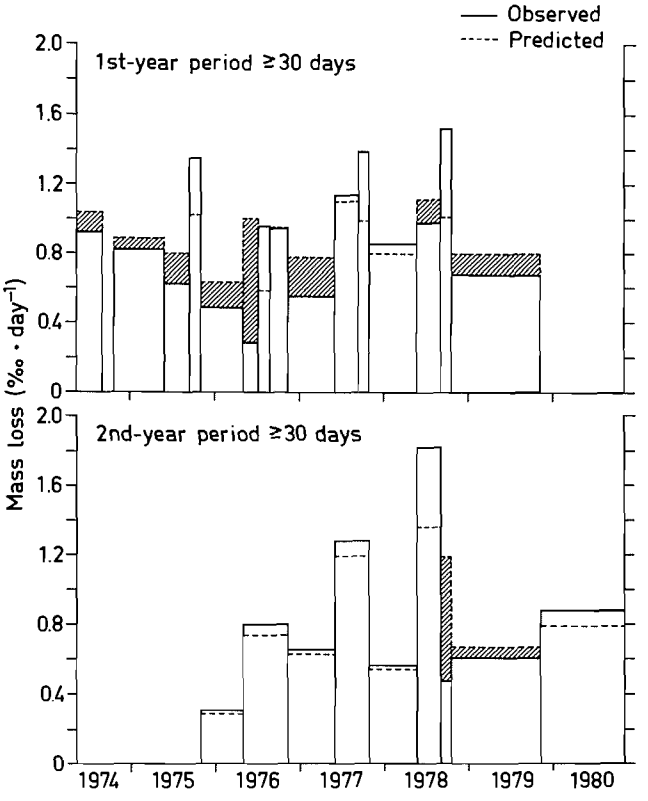

FIG. 5. Observed decomposition rates for all available observational periods for both the 1st and the 2nd year of decomposition compared with predicted litter mass loss. The empirical coefficients estimated without inertia in the abiotic functions. Shaded area shows overestimated mass loss.

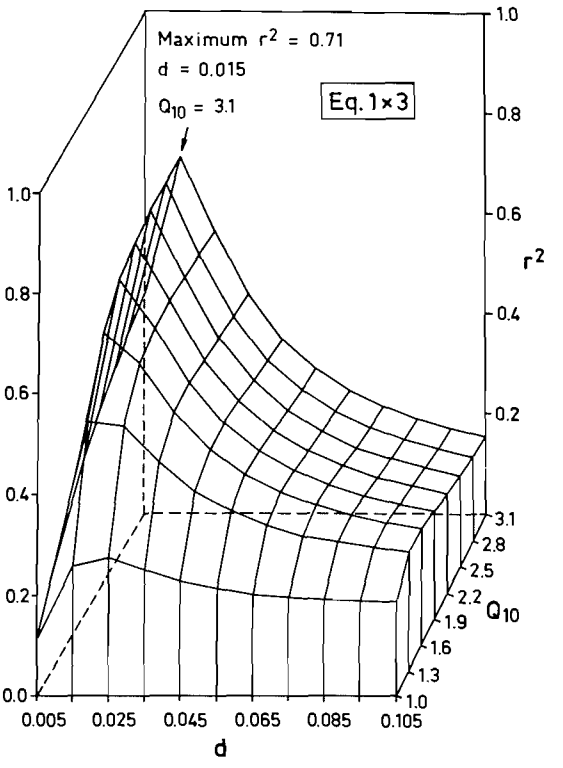

FIG. 6. Coefficients of determination (r^2) obtained with linear regression between mass losses from the 1st year using all available observations and the product of Eq. 1 and Eq. 3 reflecting water tension in combination with the inertia equation 4 for different values of the damping coefficient, d, and Q_{10}.

possible to draw conclusions from because only one additional subperiod was available in the observations. However, when the summer and the autumn of 1978 were separated, we found a low rate for the summer and a high rate for the autumn in the 1st year of decomposition, whereas the opposite was true for the 2nd year (Fig. 5). This may indicate that the delay function makes sense only for the 1st year of decomposition when a rapid ingrowth of fungal biomass takes place.

When the inertia equation ([4]) was introduced with different values on the damping coefficient d, a substantial improvement of the linear regression was obtained, especially if the Q_{10} value also was changed to higher values, for example from 1.3 to 3.1 (Fig. 6). This effect was rather similar independent of whether we used the water content equation ([2]) or the water tension equation ([3]).

The highest values of the coefficient of determination were obtained with a d-value of 0.015 giving the system a time constant of approximately 3 months. The agreement between predicted and observed decomposition for the 1st year was now improved and the same pattern with maximum decomposition for the autumn period was now seen also in the prediction (Fig. 7). This time constant may at least partly be explained by the growth time for fungal mycelium. With a dry period in, for example, the early summers of 1976 and 1979 we could expect that the fungal mycelium partly died and it may take some time for ingrowth to occur. With regard to earlier observations (Berg and Söderström 1979) the ingrowth of fungal mycelium takes such a long time that a time lag of 3 months in the model appears reasonable.

Concluding remarks

The present analysis of the relations between temperature and moisture and decomposition rates has shown that our knowledge of the actual processes in the field is limited. Important variables such as actual evapotranspiration or soil temperature could only explain about 70% of the observed variation when data from both the 1st and 2nd incubation year with periods longer than 4 months were analysed. The unfrozen part of soil water content or water tension could explain up to 90% of the same variation. When this variable, which includes an indirect effect of temperature, was combined with soil temperature, an even further improvement was obtained. Even if the number of data was limited, it may be concluded that the use of soil moisture variables should be preferred when relating decomposition to climate instead of indirect measures such as actual evapotranspiration. In both cases model calculations from climatic data must be done to obtain time series for regression analyses. The main differences consider only the amount of information on stand and soil properties which are required to calculate actual evaporation or soil climate. Unfortunately, our knowledge of these properties is rare for forests in general and at present it is restricted to only a few intensively investigated forest stands. If this information, on the other hand, can be deduced independently from easily available information on stand and soil properties, much would be gained.

The relatively low sensitivity of decomposition to soil temperature was a result of high activities during many of the winters. Also Bleak (1970) found high decomposition rates for grass and broad-leaved forbs litter under snow cover. Winter conditions appear to be equally important as summer condi-

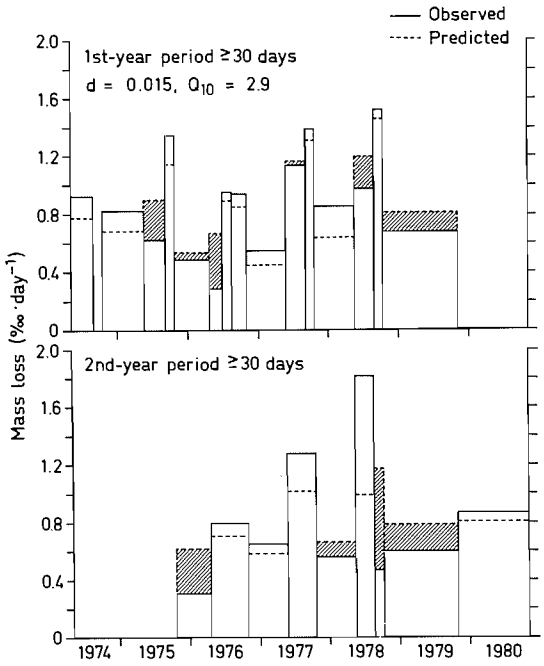

FIG. 7. Observed and predicted decomposition rates for all observational periods for both the 1st and the 2nd year of decomposition. The empirical coefficients estimated with inertia in the abiotic functions. Shaded area shows overestimated mass loss.

tions to explain variations in annual decomposition.

All the presented regressions between decomposition rates and soil climate were obtained with simulated time series of abiotic soil variables. It may be argued that uncertainties in simulated variables could have introduced substantial errors also in the obtained regressions between decomposition rate and the soil climate. However, all data originate from only one stand and the relative differences in simulated soil climate between seasons and years will probably reflect temporal variations of soil climate correctly even if the correct level may be uncertain (Jansson and Halldin 1979).

Ideally soil climate data would have been direct measurements, but in practice it will be impossible to obtain such data with a high temporal resolution and also covering long periods. The variables which were found to be most crucial in explaining variation in decomposition rate, namely the water tension or the unfrozen water content, are indeed very cumbersome to measure continuously in the field during winter conditions. Soil temperature, which on the other hand is easy to measure, showed a poor fit with observed decomposition rates.

The two widely different values for Q_{10} which were obtained in this study illustrate the problems which arise when a mechanistic response function (normally determined in the laboratory) is to be applied to field conditions. The low Q_{10} values were obtained when we considered data from periods longer than 145 days only. The sensitivity surfaces when varying Q_{10}

Appendix 1

Litter mass loss data for Scots pine needle litter

	First incubation year					
	Date (year/month/day)	Days	Accumulated mass loss (%)	Period (days)	Mass loss (%)	Decomposition rate (mass loss · day^{-1})
Set A						
1974	1974/05/02	0	0	0	—	—
	1974/09/02	123	10.4	123	10.4	0.0846
Set B						
1974–1975	1974/10/23	0	0	0	—	—
	1975/05/26	212	17.7	212	17.7	0.0835
	1950/09/12	323	23.3	111	6.8	0.0613
	1975/10/28	370	28.2	47	6.4	0.1359
Set C						
1975–1976	1975/10/29	0	0	0	—	—
	1976/04/28	182	8.8	182	8.8	0.0484
	1976/07/07	252	10.7	70	2.1	0.0298
	1976/08/25	302	14.9	50	4.7	0.0941
	1976/11/10	379	21.1	77	7.3	0.0946
Set D						
1976–1977	1976/11/11	0	0	0	—	—
	1977/06/01	202	11.1	202	11.1	0.0550
	1977/09/12	305	21.6	103	11.8	0.1147
	1977/10/27	350	26.5	45	6.3	0.1389
Set E						
1977–1978	1977/10/27	0	0	0	—	—
	1978/05/22	208	17.7	208	17.7	0.0851
	1978/08/31	309	25.9	101	10.0	0.0986
	1978/10/16	355	31.1	46	7.0	0.1526
Set F						
1978–1979	1978/11/13	0	0	0	—	—
	1979/11/07	359	26.2	359	26.2	0.0730

were, however, quite flat but with a similar shape both for the 1st and 2nd years of decomposition. This shows that either another abiotic factor like the water tension or biotic conditions dominate when temporal differences are to be explained. It does not falsify a Q_{10} value of around 3 which was found as a better estimate when shorter time periods were analysed also including an inertia in the abiotic response functions. However, the inertia was very substantial, corresponding to a time lag of approximately 3 months. This means, for example, that the favourable summer temperatures during July were smoothed out and moved to October. Again this is not a technique to estimate a true Q_{10} value, but it clearly illustrates how different the conditions can appear in the field during different periods with similar temperature conditions.

The presented technique to analyse temporal variations in decomposition will also be tested for spatial variation. Data from a number of sites in a 3000 km long transect will be compared. We feel that not until a proper explanation to variation because of abiotic influences is found, can it be possible to analyse better the variation because of biotic influences.

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incubated in a 120-year-old Scots pine forest

	Second incubation year					
	Date (year/month/day)	Days	Accumulated mass loss (%)	Period (days)	Mass loss (%)	Decomposition rate (mass loss · day^{-1})
Set B						
1975–1976	1975/10/28	370	28.2		—	—
	1976/04/28	554	32.2	184	5.6	0.0557
	1976/11/10	747	42.8	193	15.6	0.0808
Set C						
1976–1977	1976/11/10	379	21.1		—	—
	1977/06/01	579	31.5	200	13.2	0.0659
	1977/10/27	731	44.5	152	19.0	0.0950
Set D						
1977–1978	1977/10/27	350	26.5			
	1978/05/22	557	35.0	207	11.5	0.0558
	1978/08/31	658	47.0	101	18.6	0.1840
	1978/10/16	704	48.1	46	2.1	0.0452
Set E						
1978–1979	1978/10/16	355	31.1		—	—
	1979/11/07	742	53.0	387	31.8	0.0821
Set F						
1979–1980	1979/11/07	359	26.2			
	1980/10/31	717	49.2	358	31.2	0.0871

Appendix 2

SOIL water and heat model, short description

The SOIL model is based on one-dimensional numerical solutions of the partial differential equations for water and for heat. The equation for water flow is

$$[1]\quad \frac{\partial\theta}{\partial t} = \frac{\partial}{\partial z}\left(K_w\left(\frac{\partial\psi}{\partial z} + 1\right)\right) + S$$

where θ is the volumetric water content, ψ is the water tension expressed as centimetres water, K_w is the unsaturated conductivity, and S is the sink term accounting for water uptake by roots. The same type of equation is valid for heat flow including freezing–melting and convective effects of liquid flow:

$$[2]\quad \frac{\partial(C \cdot T)}{\partial t} - L\frac{\partial\theta_i}{\partial t} = \frac{\partial}{\partial z}\left(-K_h\frac{\partial T}{\partial z}\right) - C_w\frac{\partial(q_w \cdot T)}{\partial z}$$

where C is the volumetric heat capacity of soil, T is temperature, L is latent heat of freezing, θ_i is the ice content, K_h is the thermal conductivity, C_w is the volumetric heat capacity of water, and q_w is the vertical flow of water.

Boundary conditions for these equations are calculated with subroutines for interception, snow cover, and evapotranspiration.

Driving variables are daily means of precipitation, air temperature, and when available wind speed, relative humidity, global radiation, and net radiation or cloudiness. The required information on stand and soil characteristics can be varied depending on the type of application with the model.

Degree of canopy cover can be used to estimate parameters for snow melting and to calculate an appropriate soil surface temperature when snow is absent. Ideally, evapotranspiration and interception parameters can be deduced from simple stand characteristics, but these properties have so far been estimated by comparing model outputs with observations (Jansson 1980). Soil water properties would be independent measures of water characteristics and unsaturated conductivity, but these could roughly be estimated from texture and structural data (Jansson 1980). Thermal soil properties are given by the empirical functions of Kersten (1949) and de Vries (1975). Thickness of the humus layer has been found to be the most critical parameter for accurate predictions of soil temperatures.

A snow routine enables estimates of both the thickness and the density of the snow cover. Thermal conductivity is calculated from snow density and these variables are then used to calculate the soil surface temperature from measured air temperature and predicted soil temperature from the preceding time interval in the model. When snow is melting (liquid water is stored in the snow pack), the soil surface temperature is set to 0°C independent of air temperature.

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